REVUE SUISSE DE ZOOLOGIE 119 (1): 111-135; mars 2012

Bats from the wet: two new species of Tube-nosed bats (Chiroptera: Vespertilionidae) from Meghalaya, India

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Bats from the wet: two new species of Tube-nosed bats (Chiroptera: Vespertilionidae) from Meghalaya, India. - The bat fauna of Meghalaya, north-eastern India, is very diverse but still improperly known. Recent field work revealed several previously unrecorded bats, especially in the southern and eastern hill ranges known as the Khasi and Jaintia Hills. We resolve here the systematic position of two *Murina* species that belong to the "*suilla*-group" and "*cyclotis*-group", respectively, using a combination of morphological and molecular characters. Both taxa proved to be morphologically and genetically distinct from any known species and are therefore described here as new species. So far, *M. jaintiana* sp. nov. has been found both in the Jaintia Hills of eastern Meghalaya, and in the Chin Hills of north-eastern Myanmar, while *M. pluvialis* sp. nov. is only known from the dense evergreen forests of the Khasi Hills, close to the Meghalaya border with Bangladesh. During the last few decades, these areas have suffered serious habitat degradation due to deforestation associated with mining activities, and both require urgent conservation measures to preserve their unique natural resources.

Keywords: *Murina* - cryptic species - mitochondrial DNA - nuclear DNA – phylogenetics - systematics

INTRODUCTION

The north-eastern states of India lie in the foothills of the Himalaya and harbour one of the most biodiverse regions of Asia (Lamoreux *et al.*, 2006). The Meghalaya Subtropical Forests ecoregion (Wikramanaye *et al.*, 2000) is also one of the wettest ecoregions in the Indo-Pacific region. In the southern fringes of the Shillong plateau, dense evergreen forests facing the Bangladesh plains receive more than 11 meters of rainfall yearly (Rai, 2010), one of the highest recorded in the world. Many caves were formed in this region by the combination of high seasonal rainfalls and extensive limestone areas. They provide numerous roosting opportunities for troglophilous bat species. Part of the fauna of this region has been studied largely in the context of cave

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Manuscript accepted 18.01.2012

occupation, which highlighted the presence of numerous endemics in vertebrates (e.g. Kottelat *et al.*, 2007) and invertebrates (reviewed in Harries *et al.*, 2008). The bat fauna of this region has been explored on several occasions (Sinha, 1999), revealing that the Meghalaya Subtropical Forests ecoregion support several rare or otherwise unknown species elsewhere in India (Thabah & Bates, 2002, Thabah, 2005). However only a few major caves from the Garo Hills (reviewed in Sinha, 1999) and Khasi Hills (Thabah, 2005) have been adequately surveyed for bats, while the vast majority and their surrounding forested areas are still largely unexplored.

The lacunar knowledge of the bat fauna from this region is also due to the difficulty of differentiating taxa among some species-groups of Rhinolophidae, Hipposideridae and Vespertilionidae. One such difficult group is the Tube-nosed bats from the genus *Murina* (family Vespertilionidae, subfamily Murininae), which has a relatively conservative external and dental morphology. These forest bats are typically rare in collections because they require specialized trapping skills for capture (Kingston *et al.*, 2003). In classical taxonomic accounts (Corbet & Hill, 1992, Bates & Harrison, 1997), only six species of *Murina* are reported for India, four of which occur in Meghalaya (Bates & Harrison, 1997, Sinha, 1999). However, recent revisions of *Murina* species elsewhere in South-east Asia have revealed the existence of many cryptic species and inappropriate systematic arrangements (Csorba & Bates, 2005, Csorba *et al.*, 2007, Furey *et al.*, 2009, Kruskop & Eger, 2009, Kuo *et al.*, 2009, Csorba *et al.*, 2011), which suggest that *Murina* is much more diverse than currently known. For instance, the apparently widespread *M. tubinaris*, originally described from Kashmir, is now believed to be restricted to the north-west Himalayan foothills, while further east, from Nepal eastwards, a different species *Murina cineracea* occurs (Csorba *et al.*, 2011).

During an on-going survey of karstic cave formation in the Khasi and Jaintia Hills of Meghalaya organized by the "Caving in the Abode of the Clouds Project", we were invited to survey the bat fauna of caves being mapped, in an attempt to understand the significance of these karstic formations for conservation of local biodiversity. We used a combination of morphological and genetic analyses to resolve the taxonomic status of two *Murina* specimens collected in this region, which proved to be unidentifiable by external characters. We show that these specimens differ in colouration and dental characteristics compared to any described species and also differ considerably on both mitochondrial and nuclear genes from other related species. Both are consequently described here as new species.

MATERIALS AND METHODS

Bats were captured with mistnets set in forests surrounding cave entrances or across small rivers flowing out of them. In addition, we also used a 3-banks harp-trap (Austbat, Faunatech, Australia) placed in vegetation corridors to catch the smaller species which usually avoid mistnets (Kingston *et al.*, 2003). Upon capture, bats were stored temporarily in cotton bags. Prior to release, they were measured, identified and photographed, and a small biopsy punch was taken for further genetic analyses. A few specimens that did not key out to known species were taken as vouchers and kept temporarily at the Natural History Museum of Geneva, Switzerland for closer examination. These specimens will be deposited at the Zoological Survey of India's (ZSI) Shillong zoological collection.

Morphological comparisons

External measurements were taken from live specimens, dry skins or alcohol-preserved museum specimens to the nearest 0.1 mm. Craniodental measurements were taken to the nearest 0.01 mm using digital calipers under a stereo-microscope. Only fully grown adults were measured and included in the morphological comparisons. A list of abbreviations for institutions and comparative material examined is given in the Appendix. Abbreviations and definitions for measurements are FA: forearm length - from the extremity of the elbow to the extremity of the carpus with the wings folded; STOTL: total length of skull – from the anterior rim of the alveolus of the first upper incisor to the most projecting point of the occipital region; CCL: condylo-canine length – from the exoccipital condyle to the most anterior part of the canine; C^1C^1W: width across the upper canines – greatest width, taken across the outer borders of upper canines; M^3M^3W: width across the upper molars – greatest width, taken across the outer crowns of the last upper molars; ZYW: zygomatic width – greatest width of the skull across the zygomatic arches; MAW: mastoid width – greatest distance across the mastoid region; IOW: interorbital width – least width of the interorbital constriction; BCH: braincase height – from the basisphenoid at the level of the hamular processes to the highest part of the skull, including the sagittal crest (if present); CM^3L: maxillary toothrow length - from the front of upper canine to the back of the crown of the third molar; ML: mandible length – from the anterior rim of the alveolus of the first lower incisor to the most posterior part of the condyle; CM^3L: mandibular toothrow length – from the front of the lower canine to the back of the crown of the third lower molar; CPH: coronoid process height – from the tip of the coronoid process to the apex of the indentation on the inferior surface of the ramus adjacent to the angular process.

Absolute height was employed in all height comparisons for individual teeth (e.g. C^1 versus P^4). Height comparisons of hypoconids relative to entoconids were standardised by ensuring the rami of the mandible overlapped in the lateral view in each instance. Dental terminology was used after Menu (1985).

Genetic comparisons

Twelve individual bats were newly sequenced in this study. They represent 10 individuals of *Murina*, one *Kerivoula* and one *Myotis* species (Table 1). In addition, we also downloaded from the GenBank 17 reference sequences of various *Murina*, 10 of *Kerivoula*, 4 of *Harpiocephalus*, 18 of *Myotis* and 2 of *Cistugo* to serve in genetic comparisons. The genera *Kerivoula*, *Myotis* and *Cistugo* were used as increasingly divergent outgroups in phylogenetic reconstructions.

Total genomic DNA was isolated from ~25 mg tissue sample using a DNeasy Tissue Kit (Qiagen GmbH, Hilden, Germany), eluted and stored in a final volume of 200 μL AE Buffer (provided elution buffer) for further sequence analyses. The complete mitochondrial cytochrome *b* gene (cyt-b) was amplified and sequenced using the pair of primers Molcit-F (5'-AATGACATGAAAAATCACCGTTGT-3'; Ibáñez *et al.*, 2006) and CytB-H (5′-CTTTTCTGGTTTACAAGACCAG-3′; Weyeneth *et al.*, 2008). To maximize the amplification of the target gene, we used a touchdown PCR

TABLE 1 : Taxonomic sampling, geographic origin, tissue and GenBank accession numbers (cyt-b = cytochrome b gene and rag 2 = recombination-activating protein 2 gene) of the bats included in the phylogenetic reconstructions. References are : a = Anwarali Khan *et al.* (2010); b = Han *et al.* (unpublished 2009); c = Hasan & Abdullah (unpublished 2009); d = Lack *et al.* (2010); e = Ruedi & Mayer (2001); f = Sakai *et al.* (2003); g = Stadelmann *et al.* (2004a); h = Stadelmann *et al.* (2004b); i = Stadelmann *et al.* (2007); j = Thabah *et al.* (2007); k = this study.

Species	Origin	Tissue	cyt-b	Ref	rag 2	Ref
Murina aenea	Malaysia		GQ168906	*b*	-	
Mu. sp. A *A*	Phongsaly, Laos PDR	MHNG 1926.034 M1179	JQ044688	*k*	JQ044699	*k*
Mu. sp. A *B*	Nam Et, Laos PDR	CMF 980322.66	AJ841972	*h*	-	
Mu. sp. A *C*	Xuan Nha,Vietnam	IEBR XN100	JQ044700	*k*	-	
Mu. bicolor A	Taiwan		GQ168921	*b*	-	
Mu. bicolor B	Taiwan	M605	JQ044696	*k*	-	
Mu. cineracea A	Mondolkiri Province, Cambodia	HNHM 2005.81.36	GQ168915	*b*	-	
Mu. cineracea B	Phongsaly, Laos PDR	MNHN CG2006-79 M1167	JQ044694	*k*	JQ044705	*k*
Mu. cineracea C	Phongsaly, Laos PDR	MHNG 1926.035 M1172	JQ044693	*k*	JQ044704	*k*
Mu. cyclotis	Meghalaya, India	M1605	JQ044691	*k*	JQ044703	*k*
Mu. cf. *cyclotis A*	Mondolkiri Province, Cambodia	HNHM 2005.81.48	GQ168916	*b*	-	
Mu. cf. *cyclotis B*	Quang Tri Province,Vietnam	HNHM 2007.27.40	GQ168917	*b*	-	
Mu. cf. *cyclotis C*	Phongsaly, Laos PDR	MHNG 1926.033 M1209	JQ044692	*k*	JQ044706	*k*
Mu. cf. *cyclotis D*	Nam Ha, Laos PDR	CMF 980420.14	AJ841973	*h*	-	
Mu. florium	Papua New Guinea	ABTC 43635	GQ168902	*b*	-	
Mu. hilgendorfi	Hamakita, Japan		AB085733	*f*	-	
Mu. cf. *huttoni* A	Phu Khanh, Vietnam	ZMMU S-175150	JQ044695	*k*	-	
Mu. cf. *huttoni* B	Dak Lak, Vietnam	ROM 107739	GU328073	*d*	-	
Mu. jaintiana sp. nov.	East Jaintia Hills, India	MHNG 1976.072 M1619	JQ044690	*k*	JQ044702	*k*
Mu. leucogaster A	Henan, China		GQ168912	*b*	-	
Mu. leucogaster B	Beijing, China	GGJ-2006	DQ435071	*j*	-	
Mu. peninsularis	Mondolkiri Prov., Cambodia	HNHM 2005.81.16	GQ168911	*b*	-	
Mu. pluvialis sp. nov.	Cherrapunjee, India	MHNG 1976.071 M1646	JQ044689	*k*	JQ044701	*k*
Mu. puta	Taiwan		GQ168901	*b*	-	
Mu. suilla	Java, Indonesia	ABTC 48019	GQ168905	*b*	-	
Mu. tiensa A	Bac Kan Province, Vietnam	HNHM 2007.28.1	GQ168913	*b*	-	
Mu. tiensa B	Nam Et, Laos PDR	CMF 980329.19	AJ841974	*h*	-	

Outgroups						
Harpiocephalus harpia A	Nam Et, Laos PDR	ROM 118236	AJ841971	*h*	AM265701	*i*
H. harpia B	Bac Kan Province, Vietnam	HNHM 2007.27.4	GQ168923	*b*	-	
H. harpia C	Taiwan		GQ168918	*b*	-	
Kerivoula hardwickii	Sarawak, Malaysia	TK 152407	GU585657	*a*	FJ744334	*c*
K. kachinensis A	Nam Et, Laos PDR	ROM 118279*	AJ841969	*g*	-	
K. kachinensis B	Cherrapunjee, India	M1643	JQ044697	*k*	JQ044707	*k*
K. intermedia	Pahang, Malaysia	TK 152060	EU188791	*a*	FJ744343	*c*
K. cf. *lenis*	Dong Nai, Vietnam	ROM 110520*	AJ841970	*g*	-	
K. papillosa	Pahang, Malaysia	TK 152062	EU188785	*a*	FJ744327	*c*
K. pellucida	Pahang, Malaysia	TK 152055	EU188788	*a*	FJ744335	*c*
Myotis alcathoe	Franche-Comté, France	MHNG 1970.099 M1575	JQ044687	*k*	JQ044698	*k*
My. annectans	Ban Navang, Laos PDR	ROM 106376	AJ841956	*h*	AM265663	*i*
My. brandtii	Russia	NMP 49269 pb916	AM261886	*i*	AM265647	*i*
My. cf. *browni*	Mindanao, Philippines	FMNH 147067	AF376859	*e*	AM265648	*i*
My. formosus	Dong Amphan, Laos PDR	CMF 970510.6	AJ841950	*h*	AM265658	*i*
My. gracilis	Japan	KK0005	AB106609	*f*	AM265660	*i*
My. keaysi	Yucatan, Mexico	TK 13532	AF376852	*e*	GU328083	*d*
My. myotis	Spain	EBD 15969	AM261883	*i*	AM265679	*i*
My. nattereri	Thrace, Greece	M764	AF376863	*e*	AM265681	*i*
My. riparius	Pernambuco, Brasil	MVZ 185996	AF376866	*e*	AM265687	*i*
Cistugo seabrae	Goodhouse, South Africa	M977	AJ841962	*h*	GU328052	*d*

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protocol detailed in Stadelmann *et al.* (2007). In short, the initial annealing temperature was set at 50°C and decreased by one degree every other cycle, to reach the touchdown temperature at 45°C. The PCR procedure was completed by 35 cycles at 45°C annealing temperature. PCR products were submitted for sequencing to Macrogen Europe (The Netherlands).

Part of the Recombination Activating Gene 2 (Rag 2), a nuclear gene, was also sequenced using the primer-pair combination 179F (5'-CAGTTTTCTCTAAGGAYTCCTGC-3') and 1458R (5'-TTGCTATCTTCACATGCTCATTGC-3'), as described in Stadelmann *et al.* (2007).

The overlapping sequences were aligned and assembled to produce sequences of 1140 base pairs (cyt-b) or 749 bp (Rag 2), using the software Sequencher version 4.6 (Gene Codes Corp.). Sequences shorter were completed with N's to replace missing data. These new sequences were aligned with 35 cyt-b and 16 Rag 2 sequences, respectively, obtained from GenBank (Table 1). Sequencher was also used to ensure that all sequences were coding for amino acids, with no stop codons, and hence were assumed to represent orthologous genes. Sequences generated in this study have been submitted to GenBank (Accession numbers JQ044688-JQ044707; see Table 1). For measures of DNA sequence divergence, we used the K2P model of correction (K2P distance) that is commonly used for this purpose in bat systematics (see e.g. Bradley & Baker, 2001, Ibáñez *et al.*, 2006).

We used Bayesian (BA) inference and neighbour-joining (NJ) methods to separately reconstruct phylogenetic relationships for the cyt-b and Rag 2 data sets. For the BA inference and NJ method, the appropriate model of nucleotide substitutions was determined with the program MrModeltest version 2.2 (Nylander, 2004). The HKY + I + G and HKY + I models best described the cyt-b and Rag 2 data sets, respectively (cyt-b: I = 0. 0.4922, gamma distribution with shape parameter $\alpha = 0.9659$; Rag 2: I = 0.6778).

Bayesian posterior probabilities were calculated using a Metropolis-coupled, Markov chain Monte Carlo (MCMCMC) sampling approach with four simultaneous Markov chains run for 1 million generations and trees sampled every 1000 generations as implemented in the software MrBayes version 3.1.2 (Huelsenbeck & Ronquist, 2001). After the log-likelihoods of trees reached stationarity, the initial 10% of trees were discarded as burn-in and posterior probabilities were computed from the consensus of the remaining trees. NJ analyses were based on the distance matrix calculated with the DNA model of evolution selected with MrModeltest. Bootstrap analyses of 1000 replicates were performed and NJ using the same settings in MEGA version 5 (Tamura *et al.*, 2011).

RESULTS

Morphological comparisons

***Murina pluvialis* sp. nov.**

HOLOTYPE: MHNG 1976.071 (field number M1646), adult female, in spirit, skull removed, collected by MR and JB on 21 February 2011.

TYPE LOCALITY: India, Meghalaya, Khasi Hills, village of Laitkynsew, 780 ma.s.l. (metres above sea level); geographic coordinates: N 25°13', E 91°40'.

ETYMOLOGY: The name *pluvialis* ("related to rain" in Latin) refers to the habitat of the new species, which reportedly receives the highest annual rainfall in the world. The proposed English name is Rainforest tube-nosed bat.

DIAGNOSIS: The plagiopatagium is attached to the base of the claw of the outer toe. Dorsal hairs dark brown basally, the distal part reddish, the fur without shiny individual hairs; ventrally the hairs black at their basal half and light grey on the upper half. Basal area of C^1 equals that of P^4, mesostyles of M^1 and M^2 reduced but possessing distinct cusps. Forearm 36.6 mm, maxillary toothrow length 5.49 mm.

DESCRIPTION: A medium-sized species of *Murina* (Table 2). External measurements of the holotype female are: head and body 44 mm, tail 34 mm, ear 16 mm, tragus 7.5 mm, hindfoot 6.5 mm, tibia 17.6 mm and forearm 36.6 mm. On the dorsal surface the hairs show a clear banding pattern: the basal third is very dark brown, almost black, the middle part yellowish-reddish, and the tip bright red; fur without shiny guard hairs. The upper surface of uropatagium near the body is densely covered in long reddish hairs. Ventrally, hairs are dark grey for the proximal half, while the upper portion is silvery grey (Figs 1-2). The ventral side of uropatagium has sparse whitish hairs. The ear is evenly rounded and without an emargination. The plagiopatagium is attached to the very base of the claw on the outer toe (Fig. 3).

The skull is medium sized (Table 2). The braincase is domed, with rostrum not inflated. A sagittal crest is evident and runs continuously from the frontal part of the skull posteriorly to the lambda. The lambdoid crests are also well pronounced. The narial emargination is as wide as long and the zygoma are strong but lack any dorsal prominences (Figs 4-5).

The maxillary toothrows are convergent anteriorly ($C^1C^1W/M^3M^3W = 0.76$). I2 is largely obscured in the lateral view, exceeds in height I^3 and comprises less than one half of the latter's basal area. The basal area of C^1 equals that of P^4 and clearly exceeds P^4 in height. P^2 basal area and height are approximately two-thirds that of P^4. The mesostyles of M^1 and M^2 are reduced but retain distinct cusps and equal their respective paracones in height.

The lower canine (C_1) exceeds P_4 in height and is greater in basal area; P_2 is compressed antero-posteriorly, while its basal area is less than that of P_4 and nearly attains its height. The crown area of the M_1 talonid equals its trigonid while the M_2 talonid is clearly smaller than its corresponding trigonid and the entoconids of these teeth exceed their hypoconids in height. The postcristid possess a deep indentation and end posterior to the tip of the entoconid.

COMPARISONS WITH OTHER TAXA: On the basis of its dentition (I^2 obscured by I^3 in lateral view, C^1 basal area not less than that of P^4, P^2 basal area more than half that of P^4) *M. pluvialis* belongs to the "*cyclotis*-group" and is therefore readily distinguished from all members of the "*suilla*-group" currently described. Within the "*cyclotis*-group" *M. aenea* and *M. cyclotis* are characterised by the reduced cusp-pattern of molars with missing mesostyles on M^1 and M^2 and by M^1 and M^2 with a talonid much smaller in area than their respective trigonids. Among these species, only *M. cyclotis* is known to occur in continental South Asia (Srinivasulu *et al.*, 2010); this species has dorsal and ventral pelage, ear shape and craniodental measurements similar to those of

TABLE 2. Selected external and craniodental measurements (in mm) of some *Murina* species. Values are given as min–max, (n). Acronyms and definitions for measurements are given in the text.

Character	*M. pluvialis* sp. nov.	*M.* sp. A	*M. cyclotis*	*M. rozendaali*
FA	36.6	30.0-31.7 (3)	29.4-34.5 (18)	31.2-33.2 (5)
STOTL	16.4	15.63-16.09 (3)	15.66-17.62 (20)	14.81-16.05 (4))
CCL	14.5	13.75-14.21 (3)	13.56-15.41 (21)	13.09-13.97 (4)
C^1C^1W	4.21	3.86-3.91 (3)	3.73-4.68 (21)	3.78-4.31 (5)
M^3M^3W	5.52	5.24-5.30 (3)	5.08-5.89 (21)	5.25-5.50 (5)
ZYW	9.26	8.63-8.96 (3)	8.76-10.17 (21)	8.85-9.41 (5)
MAW	7.78	7.59-7.69 (3)	7.54-8.31 (21)	7.35-7.74 (5)
IOW	4.32	4.04-4.21 (3)	3.89-4.50 (22)	3.95-4.31 (5)
BCH	6.43	6.01-6.26 (3)	5.98-6.81 (21)	5.86-6.23 (5)
CM^3L	5.49	5.23-5.29 (3)	5.12-5.86 (21)	5.16-5.53 (5)
ML	11.18	10.43-10.62 (3)	10.41-12.10 (22)	10.30-10.89 (5)
CM_3L	5.93	5.7-5.84 (3)	5.56-6.26 (21)	5.76-6.14 (5)
CPH	4.02	3.64-3.73 (3)	3.77-4.78 (21)	3.33-4.03 (5)

M. pluvialis, but is readily distinguishable from the latter by its smaller forearm and especially by the above mentioned cusp arrangement on the upper molars (Fig. 6). In relation to other members of the '*cyclotis*-group' in the Indomalayan Region, *M. harrisoni*, *M. huttoni*, *M. puta* and *M. tiensa* are all much larger craniodentally with no overlap in CCL, MAW, CM^3L and CM_3L measurements (Csorba *et al.*, 2007) and none of them possess predominantly dark belly fur. The only species with similar craniodental dimensions and with distinct mesostyles on upper molars and developed talonids on lower molars in the "*cyclotis*-group" are *M.* sp. A (a currently unnamed taxon from Indochina) and *M. rozendaali* (Fig. 5).

The pelage of *M.* sp. A is basically the same being predominantly reddish brown dorsally without shiny guard hairs and dark-based ventrally but is distinguished externally by its much shorter forearm. Cranially *M.* sp. A is characterised by the lack of sagittal crest (developed in *M. pluvialis*) and dentally by the following features: CM^3L 5.30 mm or less; P^2 approximately the same height as P^4, mesostyles of M^1 and M^3 are higher than corresponding paracones; and M^2 talonid equals its trigonid (whereas *M. pluvialis* has a longer upper toothrow; P^2 reaches only two-third of P^4 in height; mesostyles and corresponding parastyles of M^1 and M^2 are subequal; and M^2 talonid decidedly smaller than the trigonid).

The pelage of *M. rozendaali* completely differs from that of *M. pluvialis* being dorsally dark brown with shining yellow or golden tips and uniformly white on the belly. In the dentition of *M. rozendaali* mesostyles are well developed and entoconids are of equal height as hypoconids, whereas in *M. pluvialis* the mesostyles of M_1 and M^2 are poorly developed and entoconids of M_1 and M_2 exceed their hypoconids in height.

DISTRIBUTION AND ECOLOGY: The holotype and currently only known specimen of *M. pluvialis* was an adult female with no external sign of reproduction, caught in the secondary, dense evergreen forest located close to the village of Laitkynsew. This forest lies on the steep slopes of the southern ridge of the Shillong plateau and receives very high orographic rains brought by the seasonal monsoons (Thabah & Bates, 2002).

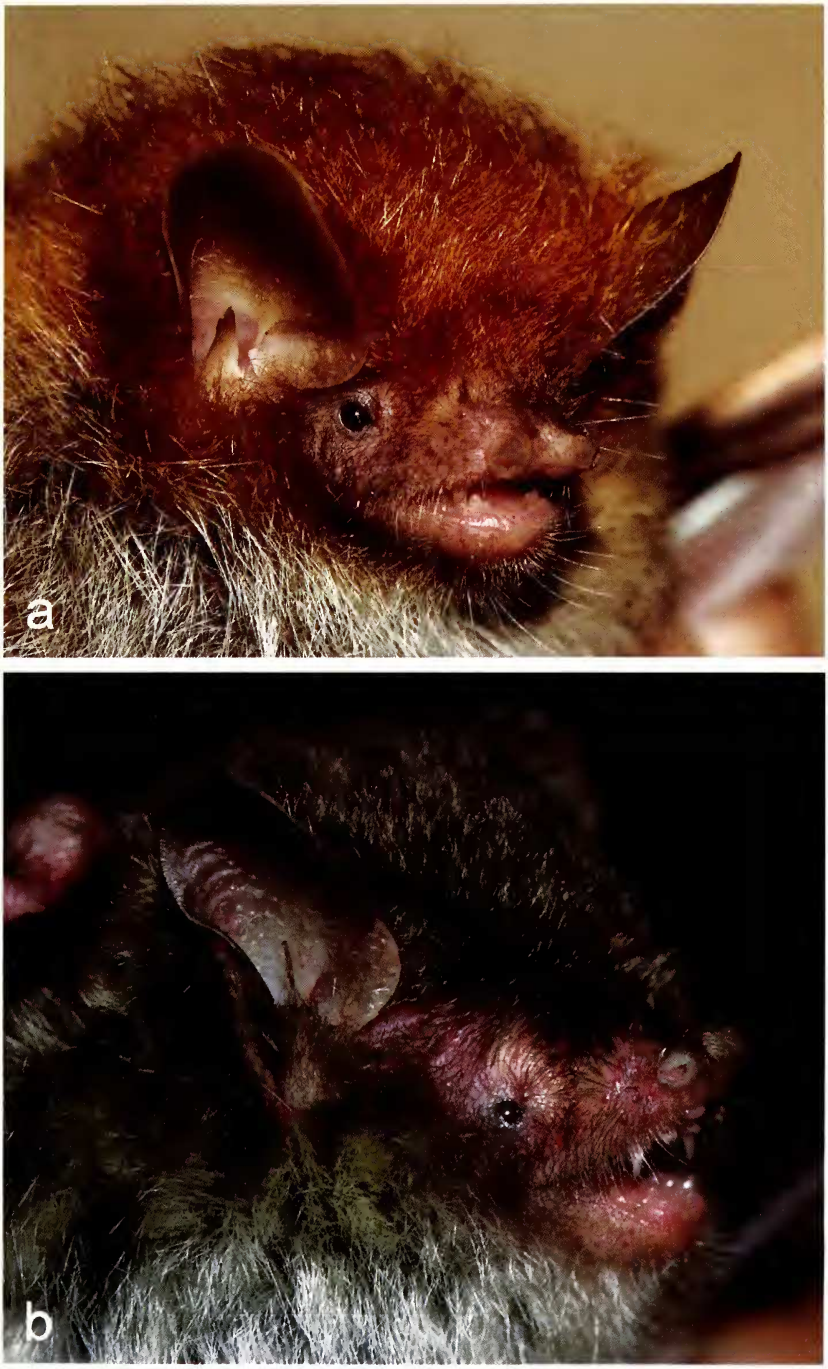

FIG. 1
Living specimens of (a) *M. pluvialis* (holotype, MHNG 1976.071) and (b) *M. jaintiana* (holotype, MHNG 1976.072).

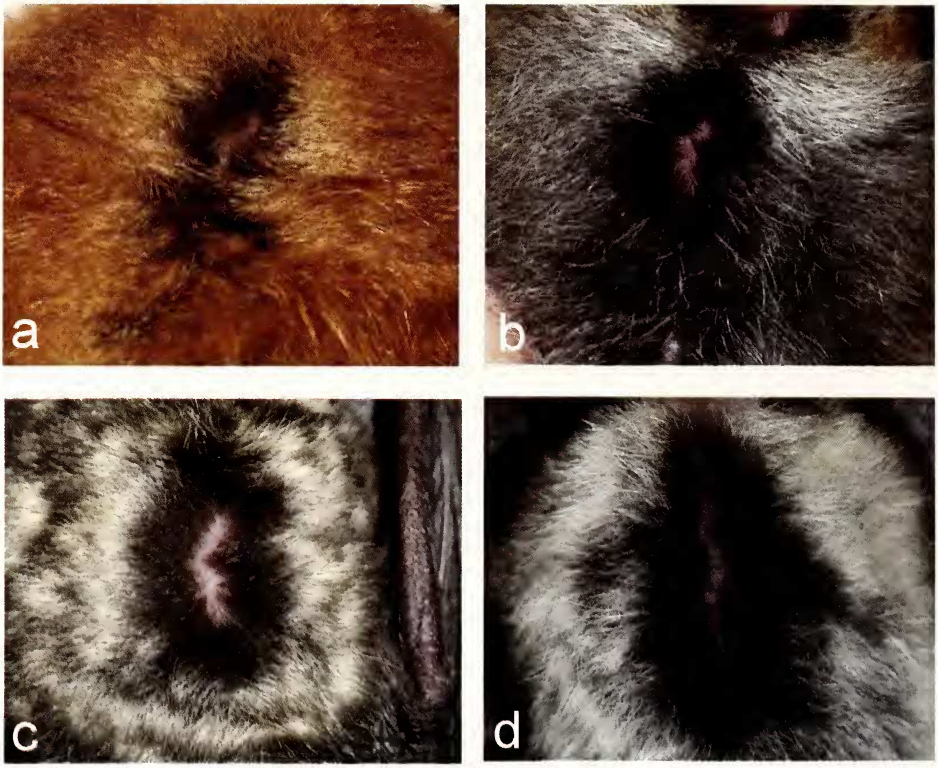

FIG. 2

Detailed view of (a) dorsal and (b) ventral pelage of *M. pluvialis* (holotype, MHNG 1976.071) and (c) dorsal and (d) ventral pelage of *M. jaintiana* (holotype, MHNG 1976.072).

The harp-trap that caught *M. pluvialis* was set up across a small path leading through a small bamboo grove intermixed with other native flora. Other bat species caught in the same harp-trap included *Rhinolophus pearsoni, R. macrotis*, *Hipposideros fulvus* and *Kerivoula kachinensis*. No other information is currently available on the ecology of *M. pluvialis*, but Bates & Harrison (1997) mention that *M.* "*cyclotis*" (i.e. the taxon with which *pluvialis* was most likely confounded) appears to have been a relatively common species in the Khasi Hills of Meghalaya, with some 30 specimens collected for the Field Museum of Natural History, Chicago (FMNH) (Bates & Harrison, 1997: p. 207).

Murina jaintiana **sp. nov.**

in part *Murina tubinaris* Bates & Harrison 1997: 207.
in part *Murina cineracea* Csorba *et al*. 2011: 896.

HOLOTYPE: MHNG 1976.072 (field number M1619), adult male, in spirit, skull removed, collected by MR and JB on 12 February 2011.

TYPE LOCALITY: India, Meghalaya, Jaintia Hills, 2.3 km east of the village of Kseh, 720 m a.s.l.; geographic coordinates: N 25°26', E 92°36'.

FIG. 3

Dorsal view of hindfoot of *M. pluvialis* (holotype, MHNG 1976.071) showing the attachment point of plagiopatagium.

REFERRED SPECIMENS: Myanmar, Chin State, Chin Hills BM(NH) 16.3.26.5., 16.3.26.7-8, 16.3.26.85-88, HNHM 2000.20.1.

ETYMOLOGY: The name refers to the local tribe, the Jaintias and the mountains named after them where the type of the new species was collected. The proposed English name is Jaintia tube-nosed bat.

DIAGNOSIS: The plagiopatagium is attached to the base of claw of the outer toe. General impression of the dorsal aspect is medium-grey; ventrally the hairs black at their basal two-third and white at the tip. Basal area of C^1 less than that of P^4, mesostyles of M^1 and M^2 rudimentary or completely missing. Forearm 29.1-31.1 mm, maxillary toothrow length 4.81-5.09 mm.

DESCRIPTION: A small-sized species of *Murina* (Table 2). External measurements of the holotype male are: head and body 40 mm, tail 33 mm, ear 13.9 mm, tragus 6.3 mm, hindfoot 6.8 mm, tibia 17.1 mm and forearm 29.1 mm. On the dorsal surface, the hairs have three distinct bands: basal half dark grey, almost black, middle part dirty white, distal end brownish-grey; there are no shiny guard hairs. The upper surface of uropatagium – especially along the tibia and near the body – is well haired with long

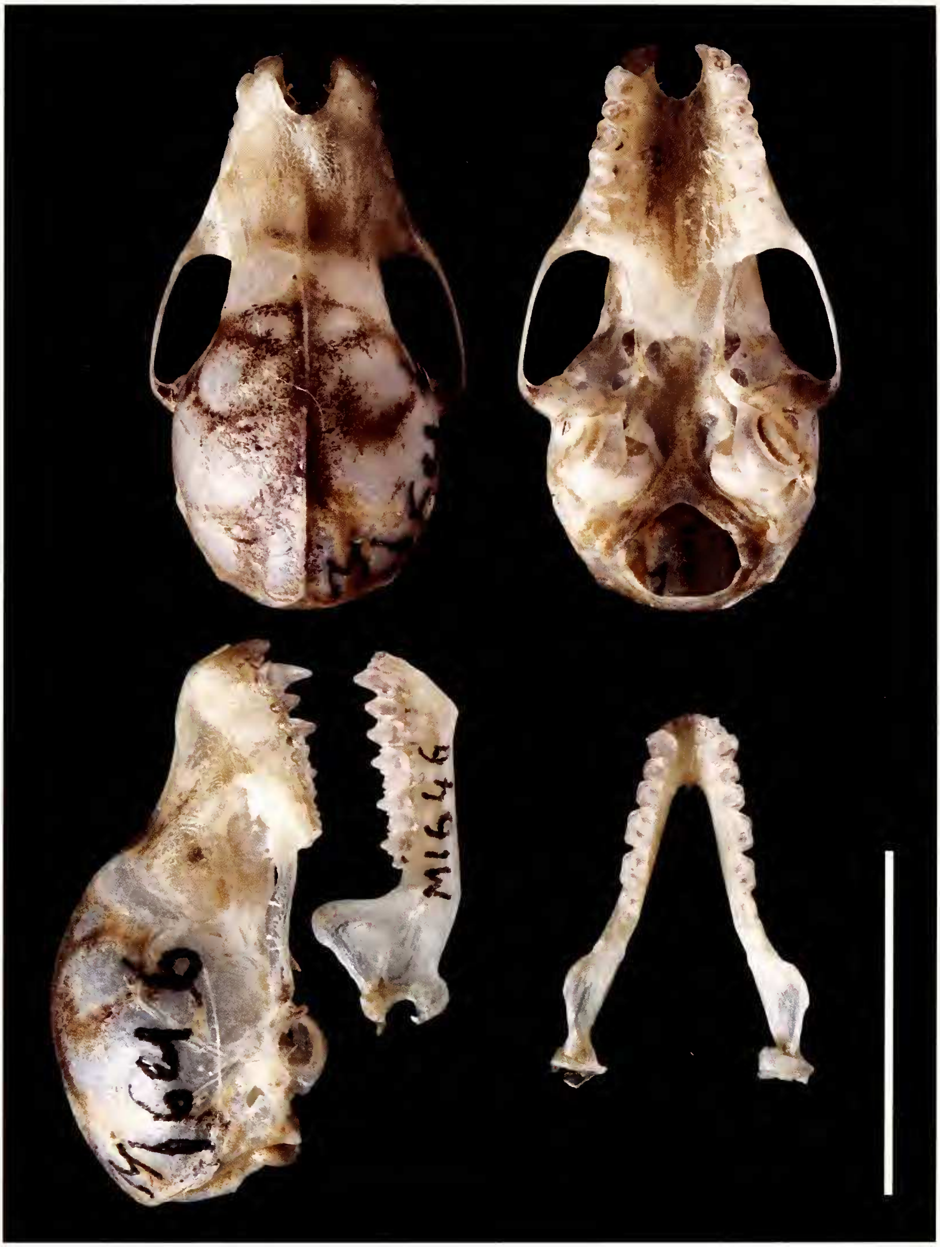

Fig. 4

Lateral, dorsal and occlusal views of skull and mandibule of *M. pluvialis* (holotype, MHNG 1976.071). Scale = 10 mm.

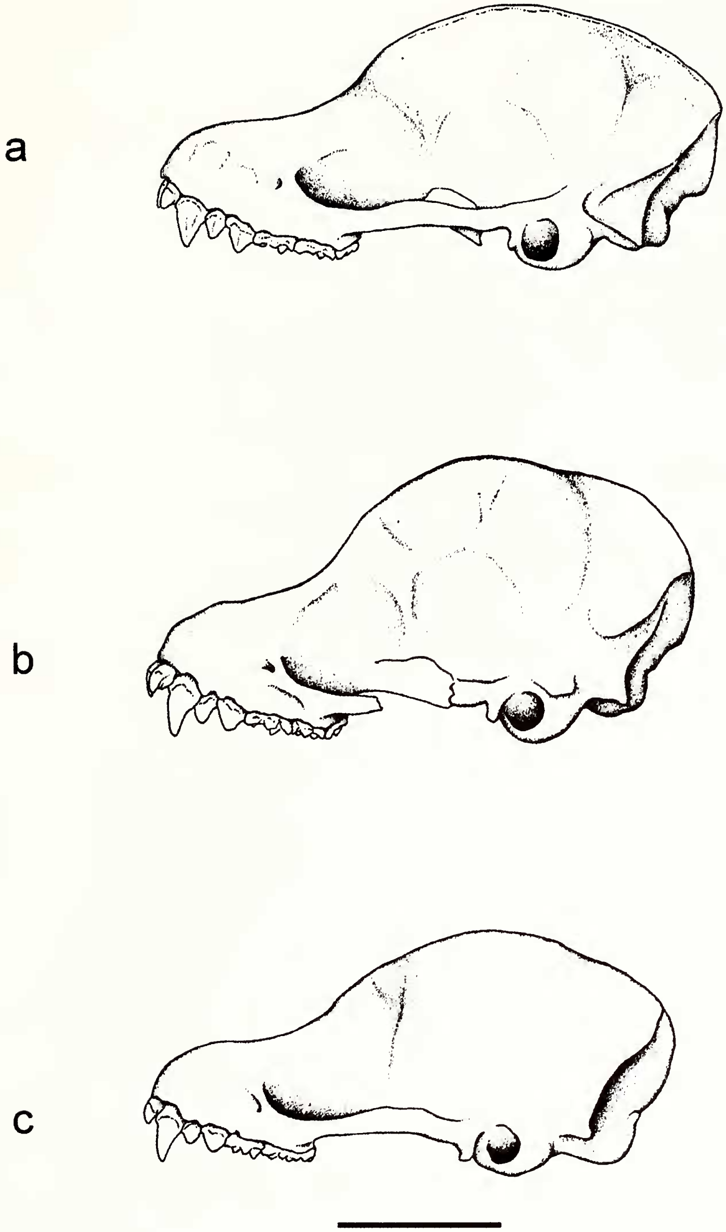

FIG. 5

Lateral views of skulls of (a) *M. pluvialis* (holotype, MHNG 1976.071); (b) *M.* sp. A (Laos, MHNG 1926.034); (c) *M. rozendaali* (holotype, BM(NH) 83.360). Scale = 5 mm.

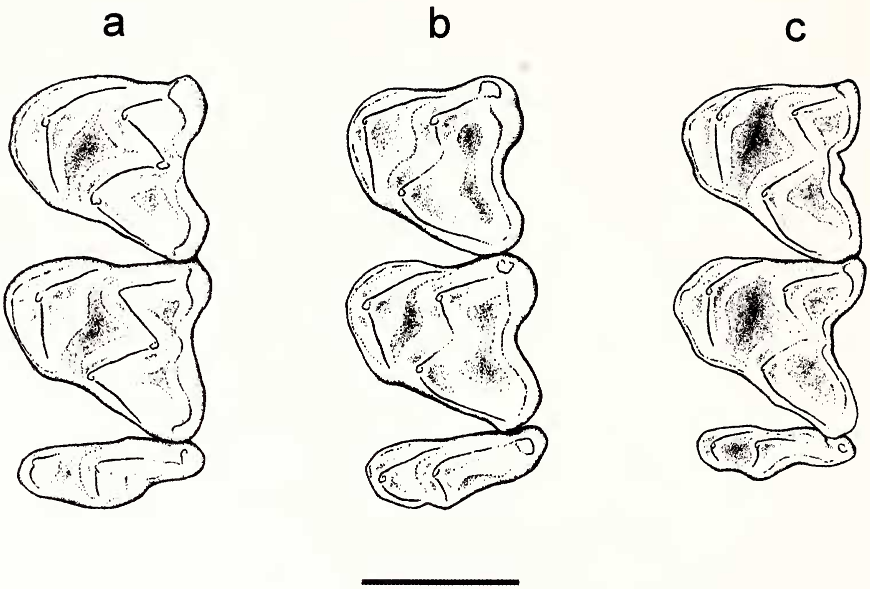

FIG. 6

Occlusal view of the upper molar row of a) *M. pluvialis* (holotype, MHNG 1976.071); (b) *M. cyclotis* (holotype, BM(NH) 9.4.4.4); (c) *M. jaintiana* (holotype, MHNG 1976.072). Scale = 1 mm.

grey-brown hairs, some of which reach beyond the free edge of the tail membrane. Ventrally, hairs are black for the proximal two-thirds, while the upper portion is a well demarcated pure white. The ventral aspect of the uropatagium has sparse whitish hairs (Figs 1-2). The ear is evenly rounded and without an emargination and the plagiopatagium is attached to the base of the claw on the outer toe.

The skull is small-sized (Table 3). The braincase is domed, and the rostrum not inflated. There is no sagittal crest and the lambdoid crests are only moderately developed. The narial emargination are as wide as long and the zygoma are strong with a low dorsal prominence (Figs 7-8).

The maxillary toothrows are convergent anteriorly (C^1C^1W/M^3M^3W = 0.69-0.71). I^2 is only partly obscured in lateral view, slightly exceeded in height by I^3 and comprises approximately one third of the latter's basal area. The basal area of C^1 is less than that of P^4, and the tooth is slenderly built and exceeds P^4 in height. The basal area of P^2 is approximately half that of P^4 and its height hardly reaches two-thirds that of P^4. The mesostyles of M^1 and M^2 are rudimentary or missing.

The lower canine (C_1) exceeds P_4 in height and is greater in basal area; P_2 basal dimensions and height are markedly less than those of P_4. M_1 and M_2 talonids equal their corresponding trigonids in area and the entoconids of these teeth exceed their hypoconids in height. The postcristid have a deep indentation and runs straight to the tip of entoconid.

TABLE 3. Selected external and craniodental measurements (in mm) of some species within the *Murina* "*suilla*" group. Values are given as min–max, (n). Acronyms and definitions for measurements are given in the text.

Character	*M. jaintiana* sp. nov.	*M. beelzebub*	*M. cineracea*	*M. tubinaris*
FA	29.1-31.1 (5)	33.7-36.3 (4)	27.5-33.8 (21)	31.0-32.9 (4)
STOTL	14.75-15.25 (6)	16.54-16.77 (4)	14.78-16.35 (22)	14.92-15.74 (6)
CCL	13.36-13.61 (2)	14.53-14.99 (4)	12.95-14.30 (23)	13.08-13.89 (5)
C^1C^1W	3.52-3.74 (6)	3.82-3.95 (4)	3.4-3.96 (23)	3.59-3.78 (5)
M^3M^3W	5.04-5.2 (6)	5.25-5.75 (4)	4.9-5.6 (23)	4.97-5.32 (5)
ZYW	8.26-8.68 (4)	8.98-9.36 (4)	8.22-9.23 (21)	8.07-8.66 (4)
MAW	7.23-7.43 (5)	7.65-8.08 (4)	7.19-7.82 (23)	7.27-7.51 (5)
IOW	4.02-4.36 (6)	4.46-4.74 (4)	4.09-4.62 (23)	4.26-4.51 (6)
BCH	5.96-6.17 (2)	6.28-6.44 (4)	5.71-6.34 (22)	5.55-5.86 (4)
CM^3L	4.81-5.09 (6)	5.41-5.54 (4)	4.84-5.36 (23)	4.88-5.19 (6)
ML	9.85-10.28 (6)	10.90-11.34 (4)	9.75-10.92 (23)	10.07-10.62 (6)
CM_3L	5.18-5.46 (6)	5.81-6.00 (4)	5.15-5.78 (23)	5.37-5.69 (6)
CPH	3.2-3.4 (6)	3.72-3.77 (4)	3.04-4.02 (23)	3.04-3.39 (4)

COMPARISONS WITH OTHER TAXA: On the basis of its dentition (I^2 only partly obscured by I^3 in lateral view, C^1 basal area decidedly less than that of P^4, P^2 basal area equals half that of P^4) *M. jaintiana* is a member of the "*suilla*-group" and is therefore readily separable from all species of the "*cyclotis*-group". Within the "*suilla*-group", only *M. beelzebub*, *M. cineracea* and *M. tubinaris* exhibit predominantly greyish dorsal fur; all other species in the group have reddish or brownish dorsal pelage without signs of any greyish-blackish tint. *M. jaintiana* is, however, easily separable from the latter three greyish species by the lack of mesostyles on M^1 and M^2 (on the other species these cusps are reduced in bulk but still clearly defined). *M. jaintiana* is further distinguished from these species by the following features.

M. beelzebub is larger in all respects with no overlap in forearm and craniodental measurements. The closely related and similar-sized *M. cineracea* differs in the ventral pelage where only the proximal half is dark brown (in *M. jaintiana* the very dark colouration extends to two-third of the length of individual hairs). In addition, the rostrum of *M. cineracea* is deep, the sagittal crest always present, albeit weak, the zygoma are stronger, C^1 and P^2 are wider at the base and more robust. In *M. jaintiana*, the rostrum is less massive in lateral view, there is no sagittal crest, the zygoma are weaker, and it has more slender C^1 and P^2 (Fig. 8).

In *M. tubinaris* the plagiopatagium is attached to the proximal phalanx of the outer toe and the zygoma are characteristically weak (whereas in *M. jaintiana* the attachment point is the base of the claw and the zygomatic arch is relatively strong) (Fig. 8).

Although it exhibits distinctive differences in colour and in general dental structure, the sympatrically occurring *M. cyclotis* is also characterised by the lack of mesostyles on M^1 and M^2. However, in the case of this species the position of paracones and metacones in relation to the protocone shows a different cusps pattern (Fig. 6).

DISTRIBUTION AND ECOLOGY: The holotype specimen of *M. jaintiana* was caught in a harp-trap set in the understory of a bamboo grove growing along a small

FIG. 7

Lateral, dorsal and occlusal views of skull and mandibule of *M. jaintiana* (holotype, MHNG 1976.072). Scale = 10 mm.

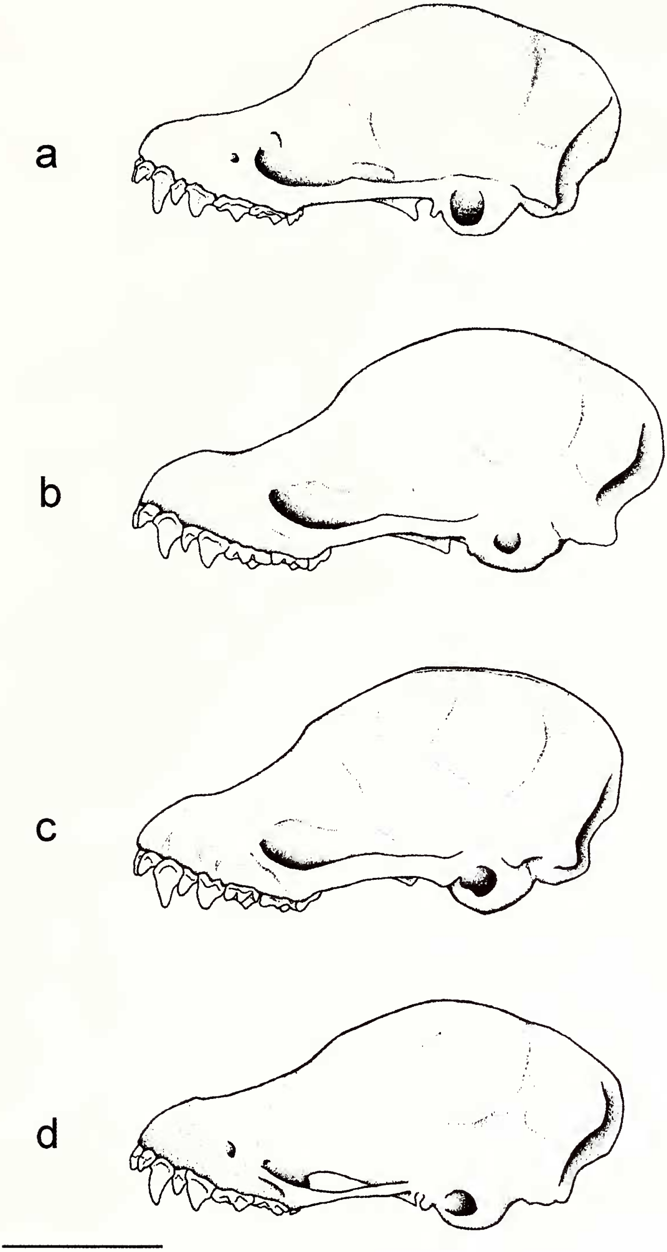

FIG. 8

Lateral views of skulls of (a) *M. jaintiana* (holotype, MHNG 1976.072); (b) *M. beelzebub* (holotype, HNHM 2007.50.24.); (c) *M. cineracea* (holotype, HNHM 2005.81.35.); (d) *M. tubinaris* (Pakistan, HNHM 99.14.7.). Scale = 5 mm.

tributary of the Kopili River. This narrow stretch of bamboos is surrounded by secondary, semi-deciduous forest located close to the village of Kseh. This forested area is heavily exploited for firewood and regularly burnt for the needs of shifting cultivation practice. Other species of bats captured in the same area include typical forest species (*Murina cyclotis*), and species more linked to cave roosts (*Rhinolophus affinis*, *R. pusillus*, *R. macrotis*, *R. pearsoni*, *R. luctus*, *Hipposideros cineraceus*, *H. larvatus*, *H. lankadiva*, *Myotis* cf. *longipes*, *Miniopterus magnater* and *Ia io*). Several karstic caves are indeed found in the same area and bats roosting there were observed using the bamboo grove as an alley to reach feeding areas along the Kopili River and surrounding forests. It is thus unclear if *M. jaintiana* was roosting, hunting or commuting through this bamboo grove. The holotype male had enlarged testis, suggesting that it was sexually active at that time of the year (February). Specimens in the Chin Hills were collected at an elevation of ca. 1500 m; according to its label, one of them was caught in a hollow in a ficus tree. The Chin Hills are covered by semi-deciduous forests similar to those found in the Jaintia Hills.

Molecular comparisons

Ten of the 12 essayed specimens yielded cyt-b and rag 2 sequences (Table 1); all sequences were in frame for coding proteins, with no stop codon or insertion that could suggest the presence of non-functional copies of these genes (paralogs). The new sequences were blasted against all available sequences in the GenBank (as of 4 November 2011), but none matched those of *M. jaintiana* or *M. pluvialis*. For the cyt-b gene, the divergence within species of *Murina* (mean K2P distance = 1.9%) was about ten times smaller than interspecific divergence (mean 17.0%), which correspond with the general pattern of divergence measured among bat taxa (Bradley & Baker, 2001, Anrawali Khan *et al.*, 2010). Likewise, the cyt-b sequence of *M. jaintiana* differed from any other *Murina* by at least 9.6%, whereas a minimum distance of 16.9% distinguished *M. pluvialis* from other taxa (Table 4).

For the more conserved nuclear rag 2 gene, these figures of divergence are lower, but still *M. jaintiana* and *M. pluvialis* had unique sequences, differing by at least 2 to 10 mutations from any other related taxa (data not shown). The mean intraspecific divergence for that gene was 0% (all conspecific sequences being identical), while they differed by a mean of 2.0% in interspecific comparisons.

Phylogenetic reconstructions were largely congruent between the two methods used (BA and NJ). The more rapidly evolving and longer (1140 bp) mitochondrial cyt-b gene expectedly yielded more resolved nodes (Fig. 9), compared to the smaller (749 bp) and more conserved fragment of nuclear rag 2 gene (Fig. 10), but the different taxon sampling in both data sets impaired further comparisons of phylogenetic performance. In all reconstructions, *M. jaintiana* appeared closely related but distinct from Southeast Asian *M. cineracea*, and also differed significantly from other sympatric species sequenced from Meghalaya (i.e. *M. pluvialis* and *M. cyclotis*). The phylogenetic position of *M. pluvialis* using the cyt-b data set and BA was unresolved within the *Murina* radiation (Fig. 9), but NJ reconstructions placed it sister to the Southeast Asian *M.* sp. A, albeit with low support (34% bootstrap). The nuclear rag 2 data set was more decisive in this situation, and clearly placed *pluvialis* sister to *M.* sp. A with 100% posterior probability (BA) or 83% bootstrap support (Fig. 10).

TABLE 4 : Mean K2P genetic distance within (diagonal, *underlined italics*) and between (below diagonal) species of *Murina* calculated for the mitochondrial cytochrome b gene. Values are given as percentages.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 *M. aena*	-															
2 *M.* sp. A	18.3	*1.7*														
3 *M. bicolor*	19.0	17.9	*0.9*													
4 *M. cineracea*	15.8	16.0	16.9	*2.3*												
5 *M.* cf. *cyclotis*	16.8	17.8	18.4	16.4	*5.3*											
6 *M. cyclotis*	16.7	16.8	19.1	16.6	12.8	-										
7 *M. florium*	15.7	18.4	17.9	14.9	19.1	18.0	-									
8 *M. hilgendorfi*	16.9	18.0	14.5	17.3	18.7	17.0	18.6	-								
9 *M.* cf. *huttoni*	19.4	18.1	18.6	18.4	17.5	16.3	19.2	18.8	-							
10 *M. jaintiana* sp. nov.	18.8	17.1	17.5	9.6	17.4	18.7	15.8	18.8	18.8	-						
11 *M. leucogaster*	18.0	18.9	9.0	16.8	16.6	18.0	16.8	14.8	19.3	17.1	*0.8*					
12 *M. peninsularis*	17.4	18.3	18.3	17.3	14.8	15.8	20.1	18.5	19.8	19.1	18.9	-				
13 *M. pluvialis* sp. nov.	17.7	16.9	19.2	17.9	18.0	17.4	18.6	19.1	17.9	18.0	20.0	17.8	-			
14 *M. puta*	20.0	18.7	17.6	18.2	19.6	18.4	19.8	18.4	8.6	20.3	18.3	18.7	20.5	-		
15 *M. suilla*	14.5	18.7	21.2	16.9	18.1	18.7	8.3	18.8	19.3	17.8	18.6	19.1	17.6	21.1	-	
16 *M. tiensa*	18.0	17.5	18.7	17.4	17.8	18.3	18.4	17.9	14.8	18.2	19.6	17.3	17.3	14.3	19.3	*0.7*

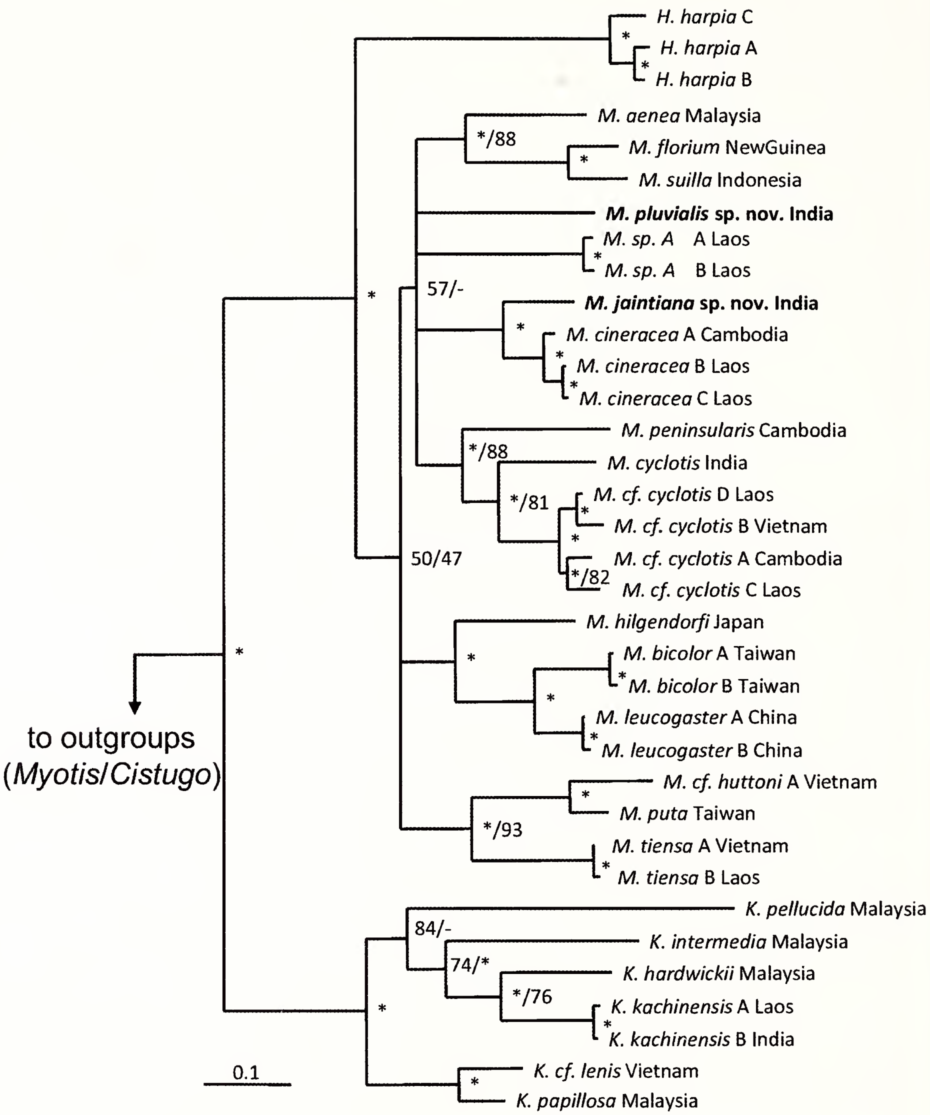

FIG. 9

Bayesian consensus tree representing the phylogenetic relationships of *Murina* (*M.*), *Kerivoula* (*K.*) and *Hapiocephalus* (*H.*) based on sequences (1140 bp) of the mitochondrial cyt-b gene. Some outgroups (genus *Myotis* and *Cistugo*) were omitted. An asterisk (*) associated to a node denotes that it is supported by at least 95% posterior probability (BA reconstructions) and /or 95% bootstrap (NJ reconstructions): other values are given as percentages. The scale bar represents 0.1 changes.

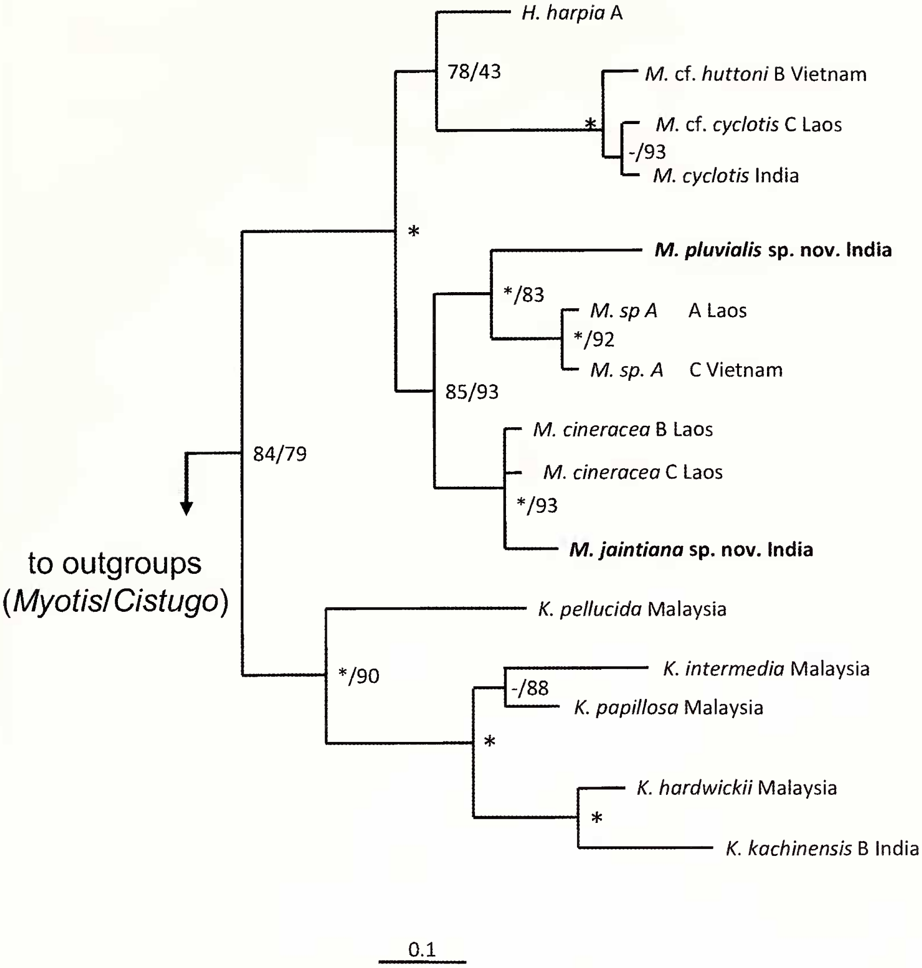

FIG. 10

Bayesian consensus tree representing the phylogenetic relationships of *Murina* (*M.*), *Kerivoula* (*K.*) and *Hapiocephalus* (*H.*) based on sequences (749 bp) of the nuclear rag 2 gene. The legend is otherwise the same as for Fig. 9.

DISCUSSION

The use of previous keys to identify Indian bats (e.g. Bates & Harrison, 1997, Sinha, 1999, Srinivasulu *et al.*, 2010) would classify *M. pluvialis* as "*M. cyclotis*" albeit with unusually large forearm and a unique mixture of whitish and dark ventral coloration; while *M. jaintiana* would key out as "*M. tubinaris*". This latter species has now been confined to the extreme western Himalayan foothills and specimens outside this area formerly regarded as belonging to this species were described as *M. cineracea* (Csorba *et al.*, 2011). While describing *M. cineracea*, the authors were already aware of the peculiar cranial and dental characters specific to the Chin Hills specimens but these morphological features alone were not considered sufficiently convincing to separate them from Indochinese *M. cineracea* at species level.

The use of molecular sequences, both from the mitochondrial and nuclear genome, and careful examination of anatomic details of vouchered specimens were essential elements which helped us resolve the taxonomic and systematic position of these enigmatic specimens. As a consequence of these taxonomic changes, the geographic area formerly regarded as occupied by "*M. tubinaris*" now harbours at least four different, apparently parapatric species, namely *M. tubinaris* (sensu stricto) in the northwest Himalayas; *M. jaintiana* sp. nov. in the Jaintia Hills, India and in the Chin Hills, Myanmar; *M. cineracea* in Indochina; and *M. beelzebub* in the Central Annamites, Indochina. The specific identity of specimens from West Bengal, Arunachal Pradesh and areas of northern Myanmar, as well as the exact distributional limits of these cryptic species still remains to be investigated.

The significance of the karstic caves found in the vicinity of capture areas of both of the new *Murina* species is unknown as yet. But because Indomalayan *Murina* in general are forest bats not associated with caves for roosting they are probably not directly affected by the continued existence of caves, but rather more dependent on the forested habitats. However, the increased demand for firewood and deforestation associated with mining activities certainly threaten the long-term existence of all forest species. Heavily exploited forests for firewood and shifting cultivation practiced in the immediate areas of the type locality of both *M. jaintiana* (Harries *et al.*, 2008) and *M. pluvialis* (Biswas, 2009) represent important threats to the survival of these (and other) bats. The use of new collection techniques and the re-examination of previously preserved museum material in the light of new external and dental characters given in this study will provide a better understanding of the exact distribution and conservation status of these new species. At least *M. jaintiana* is now recorded in the nearby forests of Myanmar, that harbour more extensive forests similar to those of Meghalaya (e.g. Struebig *et al.*, 2005), and thus may provide adequate habitats for sustainable populations of these forest bats.

The current checklist of Indian bats includes 117 species (Talmale & Pradhan, 2009), of which 58 occur in the state of Meghalaya (Bates & Harrison, 1997, Sinha, 1999, Thabah, 2005). To this figure, we add two species previously unknown to science (*M. pluvialis* and *M. jaintiana*) and record *Kerivoula kachinensis* for the first time (Table 1), which again highlight that this region needs continued studies to be properly surveyed.

ACKNOWLEDGEMENTS

We thank P. Jenkins, D. Hills and L. Tomsett (BM[NH], see Appendix for acronyms), P. J. J. Bates (HZM), C. Smeenk (RMNH), N. Furey (FFI Cambodia Program) and Nguyen Truong Son and Vu Dinh Thong (IEBR) for kindly providing access to specimens under their care. The taxonomic work of GC was supported by the SYNTHESYS Integrated Infrastructure Initiative Grant and by the Collection Study Grant to MHNG. We are indebted to B. D. Kharpran Daly from the Meghalaya Adventurers Association, T. Arbenz, O. Chachula and other team members of the Caving in the Abode of the Clouds Project 2011 for providing access to the forests and help in the field work and to A. Honfi for the final elaboration of the drawings. N. Furey and A. Thabah reviewed the manuscript, which we thank for their expert and constructive comments.

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APPENDIX

INSTITUTIONAL ABBREVIATIONS: Specimens and tissue samples included in this study are held in the collections of BM(NH): The Natural History Museum, London, UK, formerly British Museum (Natural History). – CMF: Charles M. Francis collection, Canada). – EBD: Estacion Biologica de Doñana, Sevilla, Spain). – FMNH: Field Museum of Natural History, Chicago, USA. – HNHM: Hungarian Natural History Museum, Budapest, Hungary. – HZM: Harrison Institute, Sevenoaks, UK, formerly Harrison Zoological Museum. – IEBR: Institute of Ecology and Biological Resources, Hanoi, Vietnam. – KK: Kuniko Kawai collection, Japan. – M: Manuel Ruedi collection, Switzerland. – MHNG: Muséum d'histoire naturelle, Geneva, Switzerland. – MVZ: Museum of Vertebrate Zoology, Berkeley, USA. – NF: Kim Hy Nature Reserve Collection, Vietnam. – NMP: National Museum Prague, Prague, Czech Republic. – RMNH: National Museum of Natural History, Leiden, the Netherlands, formerly Rijksmuseum van Natuurlijke Historie. – ROM: Royal Ontario Museum, Toronto, Canada; TK. – Museum of Texas Tech University, Texas, USA. – ZMMU: Zoological Museum of Moscow University, Moscow, Russia.

Comparative material examined

Murina aenea: MALAYSIA (Pahang) – BM(NH) 64.770 (holotype).
Murina sp. A: LAOS – MHNG 1926.034; VIETNAM – HNHM 2008.23.10., IEBR XN100.
Murina beelzebub: VIETNAM – HNHM 2007.50.24. (holotype), HNHM 2007.50.6., 2007.50.7., HZM 3.32053.
Murina cineracea: CAMBODIA – HNHM 2005.81.35. (holotype), 2005.84.4., 2005.81.36., 2005.81.49.-53., 2006.34.40.; LAOS – MHNG 1926.035; VIETNAM – HNHM 2000.84.7., HZM 1.31524, 1.31780, IEBR QHB005, TS12, 32CMR, T210708.1, T251107.5, T290708.8, T250607.1, T112, T83, VN01-C4; NF 071206.2, 250407.1.
Murina cyclotis: CAMBODIA – HNHM 2005.81.33., 2005.81.48., 2006.34.2., 2006.34.34., 2006.34.38., 2007.49.10.; INDIA – BM(NH) 9.4.4.4 (holotype), 15.9.1.38, 16.3.25.28-29, 20.6.24.1; LAOS – MHNG 1926.033; MYANMAR – BM(NH) 16.3.26.3-4, 16.3.26.89, 50.484; NEPAL – HNHM 98.7.3.; THAILAND – BM(NH) 78.2383, 82.165; VIETNAM – BM(NH) 1997.384, HNHM 2000.84.3., 98.3.3., IEBR NTS1597.
Murina harrisoni: Cambodia – HZM 1.36316 (holotype).
Murina huttoni: INDIA – BM(NH) 79.11.21.685 (holotype).
Murina peninsularis: MALAYSIA (Pahang) – BM(NH) 64.771 (holotype).
Murina puta: TAIWAN – HNHM 98.19.4., 98.19.6.
Murina rozendaali: MALAYSIA, SABAH – BM(NH) 83.36 (holotype), 84.2025, 1999.300; RMNH 32235; PENINSULAR MALAYSIA – BM(NH) 1999.301.
Murina tiensa: VIETNAM – HZM 2.38178 (holotype).
Murina tubinaris: INDIA (Himachal Pradesh) – MHNG 1926.060; “KASHMIR” – BM(NH) 3.9.29.2; PAKISTAN – BM(NH) 65.1023, HNHM 99.14.6. HNHM 99.14.7., BM(NH) 1999.151.